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CONTINUOUS LAYING BY AMERICAN COOTS IN RESPONSE TO PARTIAL CLUTCH REMOVAL AND TOTAL CLUTCH LOSS

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ABSTRACT.—The ability of American Coots (*Fulica americana*) to produce additional eggs was studied by experimentally removing six eggs from the clutch during laying (while always maintaining at least three eggs in the nest), and by removing entire clutches during laying to force birds to renest. Coots responded to partial (six-egg) clutch removals by laying an average of 11.5 total eggs, which represents a slight though significant increase over the mean control clutch size of 10.5. Despite this modest increase in mean clutch size, there was a pronounced increase in the proportion of coots producing supernormal clutches (i.e. ≥ 13 eggs; 26% of removal clutches vs. 8% of control clutches). Egg production was not affected by food availability, as coots with access to supplemental food were no more likely to respond to partial clutch removals than were coots from unsupplemented territories. In response to total clutch loss during laying, most coots (99/119; 83.2%) initiated a continuation clutch. Virtually all continuation clutches (92.4%) were initiated within five days ($\bar{x} = 1.5 \pm \text{SD of } 2.2$ days). Continuation clutches were no smaller than normal clutches, even though continuation nesters had produced several previous eggs. In 1990 and 1991, the total number of eggs produced by continuation nesters (all consecutive nests combined) averaged 15.8 ± 8.2 and 12.8 ± 5.2 , respectively, compared to 9.8 ± 1.5 and 11.0 ± 2.1 eggs per clutch in initial undisturbed nests. One continuation nester produced a remarkable 35 eggs in 37 days (four consecutive nests plus two parasitic eggs). Neither egg size nor nesting success were reduced among continuation nesters. Collectively, these data provide strong evidence against the egg-formation hypothesis, which has been invoked to explain both clutch- and egg-size variation in American Coots. These data demonstrate that continuation nesting may provide a better means than partial clutch removals of testing egg-formation capabilities in birds. Received 5 March 1991, accepted 13 January 1992.

ACCORDING to Klomp (1970:2-3), the number of eggs laid per clutch by determinate layers is unequivocally limited by the number of follicles that initiate development before laying begins. Among indeterminate layers, the number

of eggs laid per clutch is not determined by the number of initially developing follicles, but is instead regulated by an unknown feedback mechanism that causes additional follicles to develop and/or previously developing follicles to be resorbed during the egg-laying period (Klomp 1970:4-5). One frequently used method of distinguishing between determinate and indeterminate layers is to manipulate the number of eggs present in the nest during egg laying

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(reviewed in Kennedy 1991). Determinate layers should not alter the total number of eggs that they lay, whereas indeterminate layers will often respond to experimental egg additions or removals by laying fewer or more total eggs, respectively (Cole 1917 in Klomp 1970).

The egg-formation hypothesis suggests that clutch size in some species of birds is limited by the ability of laying females to form additional eggs (Lack 1967, Ryder 1970, Ankney and MacInnes 1978). Results from egg-removal experiments are often cited as evidence for or against this hypothesis (Lack 1947, Winkler and Walters 1983, Rohwer 1984, 1986, Briggs 1985, Duncan 1986, Arnold 1990a). Clearly, if egg removals can induce females to produce more eggs than are found in a typical clutch, at a normal rate of egg laying, and with no dire consequences later in the breeding cycle (i.e. an inability to complete incubation due to physical exhaustion), then one could conclude that clutch size is not limited by the ability of females to produce eggs. Few egg-removal experiments have generated such clear-cut results, however. Typically, females do not alter their clutch size in response to egg removals, or they respond by replacing only a few of the eggs that were removed (reviewed in Kennedy 1991). Such data are ambiguous; they do not indicate whether females were incapable of laying additional eggs (as implied by the egg-formation hypothesis), or simply unstimulated to lay more eggs (Klomp 1970). Thus, response of a bird to egg removal demonstrates indeterminate laying, but lack of response does not demonstrate determinate laying; it only demonstrates that the number of eggs present in the nest during laying does not proximately affect clutch size (Klomp 1970, Briggs 1985).

Rohwer (1984, 1986) noted that laying female ducks (prairie-nesting *Anas* and *Aythya*) do not respond to experimental egg removals by producing additional eggs, but a few females that lose their nests during laying will immediately initiate a continuation nest and proceed to lay a normal complement of eggs in the new nest, without interrupting the normal rate of egg laying. This phenomenon has rarely been observed among waterfowl (see Rohwer 1986), but when it has occurred, females have laid many more consecutive eggs than are ever found in a normal clutch. For example, Gates (1962) documented 22 consecutive daily eggs in three successive nests of a marked female Gadwall

(*Anas strepera*), but clutch size in this population averaged 10.1 and did not exceed 12 in a sample of 43 nests (Gates 1962:table 6). Observations such as this would seem to provide a powerful rejection of the egg-formation hypothesis (see Arnold and Rohwer 1991), but continuation laying has been recorded so infrequently among waterfowl (and there have been so few opportunities to observe continuation laying) that it would be premature to draw firm conclusions from the few available records.

In this paper, I use two sources of data to assess the ability of American Coots (*Fulica americana*, hereafter "coots") to produce additional eggs: (1) total eggs laid in response to partial clutch removals; and (2) ability to produce continuation nests following total clutch loss during laying. Previous authors have implied that clutch sizes and/or egg sizes of coots were limited by the availability of nutrients for egg-laying females (Alisauskas and Ankney 1985, Alisauskas 1986, Hill 1988, 1989, Briggs 1989). If this were true, I predicted that: (1) females would not respond to partial or total clutch removals by producing more total sequential eggs than are found in a typical clutch; or (2) if females did respond by laying more total eggs, they would either have to compromise the size of their eggs (e.g. Rohwer and Eisenhauer 1989), or they would be unlikely to successfully complete incubation (e.g. Ankney and MacInnes 1978).

METHODS

I conducted egg-removal experiments during four field seasons (1985–1988) on a study area near Minnedosa, Manitoba (50°10'N, 99°47'W). The study area consisted of numerous small wetlands (~0.1 to 3.0 ha) that were inhabited by 1 to 21 pairs of breeding coots. Egg removals started with the fourth-laid egg and continued daily through the ninth-laid egg; that is, six eggs were removed from each clutch, at a rate of one egg per day (the typical laying rate; Arnold 1990b), unless the laying female failed to produce nine or more eggs. Hence, until they laid 11 or more eggs, laying birds always returned to find up to 3 eggs in their nests. I began removals with the fourth-laid egg because manipulation of nest contents when fewer eggs are present can result in high rates of abandonment (Arnold, pers. observ.; see also Livezey 1980, Rohwer 1984, 1986). Coots typically have four to six simultaneously developing follicles (Alisauskas and Ankney 1985, Arnold 1990b), and clutch sizes at Minnedosa are most commonly 8 to 12 eggs (see Table 1). Thus, coots should have had plenty of time to

TABLE 1. Number of eggs laid by American Coots in response to experimental removal of six eggs during laying.

Sample ^a	Treatment	Number of nests for clutch size																		F _{max} -test ^b		ANOVA ^c		ANCOVA ^d		ANCOVA ^e	
		3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	F	P	F	P	F	P	F	P	
		$\bar{x} \pm 1 \text{ SD } (n)$																		F	P	F	P	F	P	F	P
85UNFED	Control					1			5	3	1	2	1	1	1			11.00 ± 1.63 (13)	2.06	ns	4.36	0.05	7.21	0.02 ^f	7.33	0.016	
	Removal						3	2	8	19	23	21	13	4	1			12.86 ± 2.34 (7)	3.66	<0.05	7.80	0.006	5.26	0.03 ^f	4.74	0.03	
86UNFED	Control																	11.11 ± 1.61 (94)									
	Removal																	12.67 ± 3.08 (12)									
87UNFED	Control				1	1	5	6	8	1	2							9.25 ± 1.42 (24)	1.53	ns	0.37	0.55	0.12	0.73	3.23	0.08	
	Removal																	8.89 ± 1.76 (9)									
87TROUT	Control																	9.38 ± 2.19 (16)	0.62	ns	0.00	0.95	0.28	0.61	0.46	0.51	
	Removal																	9.43 ± 1.72 (7)									
87CORN	Control																	10.77 ± 1.09 (13)	5.60	0.05	0.02	0.90	0.75	0.40	0.96	0.34	
	Removal																	10.67 ± 2.58 (6)									
87C+T	Control																	10.31 ± 1.38 (13)	2.97	ns	0.30	0.59	0.64	0.43	0.35	0.56	
	Removal																	10.75 ± 2.38 (8)									
87POOLED ^g	Control				3	2	10	12	15	15	6	3						9.93 ± 1.67 (66)	1.67	ns	0.04	0.85	1.25	0.27	1.18	0.28	
	Removal																	9.91 ± 2.25 (30)									
88UNFED	Control																	8.91 ± 1.76 (131)	1.91	ns	1.16	0.28	4.89	0.03	0.09	0.77	
	Removal																	9.50 ± 2.43 (12)									
88MIX	Control																	9.75 ± 1.58 (121)	2.60	ns	2.54	0.11	5.23	0.02 ^f	4.59	0.03	
	Removal																	10.67 ± 2.55 (9)									
88POOLED ^h	Control																	9.33 ± 1.73 (252)	2.07	ns	2.84	0.09	9.77	0.002	1.91	0.17	
	Removal																	10.06 ± 2.49 (21)									
ALL DATA ⁱ	Control																	10.50 ± 1.84 (425)	2.17	<0.01	11.00	0.001	19.84	0.0001	0.11	0.74	
	Removal																	11.54 ± 2.71 (70)									

^a Explanation of sample group mnemonics: numerals designate year of study (e.g. 85). UNFED = pairs without supplemental food, CORN = pairs receiving corn, TROUT = pairs receiving trout chow, C+T = pairs receiving both corn and trout chow, MIX = pairs receiving mixed food supplement, POOLED = supplemented and unsupplemented pairs combined.

^b F_{max} = s² removal/s² control.

^c ANOVA of H₀: \bar{x} removal = \bar{x} control (i.e. t-test).

^d ANCOVA of H₀: \bar{x} removal = \bar{x} control (i.e. homogeneity of intercepts, or removal effect with laying date used as covariate).

^e ANCOVA of H₀: b removal = b control (i.e. homogeneity of slopes, or removal-by-laying-date interaction).

^f Significant removal-by-laying-date interaction included in model.

^g 1987 sample groups combined due to lack of removal-by-supplemental-food interactions (F ≤ 3.02, P ≥ 0.09). Means are least squares estimates controlling for significant effect of supplemental corn (F = 14.00, P = 0.0003). Standard deviations based on raw data.

^h 1988 sample groups combined due to lack of removal-by-supplemental-food interactions (F = 0.07, P = 0.79). Means are least squares estimates controlling for significant effect of supplemental food (F = 16.86, P < 0.0001).

ⁱ 1985-1988 sample groups combined. Means are least squares estimates controlling for effects of year (F = 28.72, P < 0.0001), food supplements (F = 23.18, P < 0.0001), and year-by-egg-removal interaction (F = 2.49, P = 0.06); no other interactions were significant (F ≤ 0.64, P ≥ 0.42).

respond to egg removals by developing additional follicles, if such a response was part of their normal nesting behavior (see also Rohwer 1986). Control clutches were nests found during the same time period as removal clutches (clutch size declines seasonally in coots [Alisauskas and Ankney 1985, Arnold 1990b]; hence, removal and control clutches should have similar initiation dates). For 1985 through 1987, control nests were visited daily to mimic the level of investigator disturbance experienced at removal nests, but daily visits to control nests were not continued in 1988. In 1985 and 1986, I also conducted a small number of experimental egg additions. This involved adding six eggs to the clutch, at a rate of one to three eggs per day, so that all six eggs were added by the time the host female had laid her sixth or seventh egg.

In 1987 and 1988, supplemental food was available to large samples of coots during egg laying, including birds from removal and control nests. In 1987, supplemental food included cracked corn and trout chow, which were provided independently in a 2×2 factorial design (i.e. \pm corn, \pm trout chow). Corn is extremely high in nitrogen-free extract (i.e. carbohydrate, 80.4% of dry weight) and is an excellent diet for lipogenesis (Alisauskas et al. 1988), whereas trout chow is high ($\geq 40\%$) in crude animal protein (Arnold 1990b:appendix 1). These food supplements were selected to independently assess lipid (corn) and protein (trout chow) limitation during egg laying (Alisauskas and Ankney 1985, Drobney and Fredrickson 1985, Ankney and Afton 1988, Briggs 1989, Hill 1989). Coots readily consumed supplemental corn, but reluctantly consumed trout chow. I could not determine if this was in response to specific nutrient needs (i.e. lipid limitation, rather than protein limitation; Drobney and Fredrickson 1985, Ankney and Afton 1988), or due to differential palatability. But because adult coots are not normally carnivorous (Jones 1940), I changed the composition of supplemental food in 1988 in attempt to provide a more palatable diet. In 1988, supplemental food consisted of a 20:10:10:1:1 mixture of cracked corn, layer diet for chickens (protein content $\geq 18\%$), rabbit pellets (plant protein, $\geq 18\%$), oyster shell (calcium supplement), and grit (to assist with mechanical breakdown of food in the gizzard).

I studied continuation nesting at the same study site in 1990 and 1991. In 1991, supplemental food (same mixture as in 1988) was available to approximately one-half of the coot pairs. Data on continuation nesting came from two sources: (1) manipulative data from experimental clutch removals, in which I removed all eggs from laying-stage coot nests to induce renesting; and (2) observational data from clutches that were naturally destroyed or abandoned during egg laying. Clutch manipulations were conducted with the larger objective of determining renesting intervals in relation to stage of the initial nest

at the time of destruction (e.g. Doty et al. 1984), so clutch removals were not standardized with respect to number of eggs laid. Data used in this paper are from clutches that I removed during the laying stage (2–11 eggs laid). At completion, most initial clutches on my study area contained 8 to 12 eggs (range 4–18). Thus, some coots had undoubtedly laid the final egg of their clutch on the day that I collected their eggs (i.e. these birds were incubating, not laying), but I had no way of assessing whether this was the case. Manipulations were completed before 1000 to allow coots as much time as possible to construct a new nest before their next egg was due to be laid. I removed only one clutch per coot pair, but subsequent clutches sometimes were destroyed or abandoned during laying. For clutches that were destroyed naturally, there was often some ambiguity as to exactly when nest destruction took place. For these clutches, I assumed that destruction had occurred at the earliest possible date. Hence, estimates of total eggs laid are minimal and estimates of renesting intervals are maximal. Some coots produced two to four continuation nests in response to repeated nest failures. These instances of multiple continuation nests occurred because some coots were extremely sensitive to investigator disturbance and abandoned their new clutch as soon as I discovered it. This continued to occur even after I ceased flagging nests and marking eggs, so I believe it was my physical presence at the nest that caused these birds to abandon. Nest bowls were not disturbed during experimental clutch removals, and often remained intact following natural clutch destruction, but only 1 of 73 coots renested in the same nest bowl following total clutch loss (this occurred more regularly following partial clutch removal; see also Fredrickson 1969, Hill 1986). I assigned continuation nests to particular females (who were not individually banded) by a combination of criteria, including timing of nest initiation in relation to destruction of a previous nest (i.e. a continuation nest had to have been initiated after an earlier nest was destroyed), proximity to a previously destroyed nest (usually ≤ 40 m), and most importantly, visual characteristics of the respective eggs (i.e. shell color and spotting pattern; Arnold 1990b:appendix 2). In blind performance trials to assess my accuracy at recognizing individual coots according to characteristics of their eggs, I achieved approximately 90% correct identification in three of four experiments (Arnold 1990b). Statistical analysis of egg-size repeatability (see below) provided further evidence that I was assigning continuation clutches to the correct individuals. Therefore, I am confident that virtually all continuation nests were identified correctly. In a few instances (all from 1991) in which continuation nests could not have been discovered because subsequent nest searches were not conducted, I inferred that females had renested if an unmarked newly hatched brood was observed within the former nesting territory (all other broods on these

wetlands had individually color-marked chicks). In these instances, the brood could have been produced by a replacement female, rather than the initial nesting female, but observations from other territories (for which all nests were discovered and egg characteristics were compared) suggest that replacement females would have been rare.

Three out of 73 females laid eggs parasitically in nests of other coots during the interval between destruction of their initial nest and initiation of their replacement nest (see Appendix footnotes). In all three cases, these eggs were recognized as being parasitic on the basis of faster than normal rates of egg deposition (i.e. 2 eggs/day) in the hosts' nests (e.g. Rohwer and Freeman 1989), and they were attributed to a particular parasitic female on the basis of egg characteristics (Arnold 1990b; see also Gibbons 1986, Lyon 1991, Møller and Petrie 1991). In one case the presumed parasite was the only other nesting female on the wetland, in another case there were two other females present, and in the third case there were 11 other nesting females, but the presumed parasite occupied the adjacent territory.

Clutch size refers to the number of eggs laid in a single nest bowl in a single laying sequence by a single coot (parasitic eggs that could be recognized by supernormal laying rates or egg characteristics were excluded). A laying sequence was defined as a series of eggs produced by a single female in one or more nest bowls and separated by no more than 48 h between consecutively laid eggs (laying coots typically lay one egg per day, but laying skips occur on approximately 3% of all potential laying days; Arnold 1990b:table 3.8). Clutch size was considered complete if no new egg was added for two consecutive days, provided that eggs in the nest were warm to the touch (i.e. warmer than ambient temperature) and, hence, being incubated by at least one parent and not simply abandoned during laying (abandoned clutches were excluded in the egg-removal experiment). Clutch size at removal nests refers to total eggs laid and, therefore, includes the six eggs that were experimentally removed. At egg-addition nests, clutch size does not include the six experimentally added eggs. For the continuation-nesting experiment, clutch size refers to the number of eggs laid in the replacement clutch, if it was completed and subsequently incubated. Total eggs refers to the total number of eggs laid in one or more nests by females with nests that were destroyed during laying, whether or not such females produced a continuation nest, and whether or not all eggs were part of a single laying sequence. For example, a female whose first clutch was destroyed at the six-egg stage and who did not subsequently reneest would have produced six total eggs, whereas a female whose first clutch was destroyed at the seven-egg stage and who went on to lay a nine-egg replacement clutch (with or without interrupting the original laying sequence) would have produced 16 total eggs. I defined se-

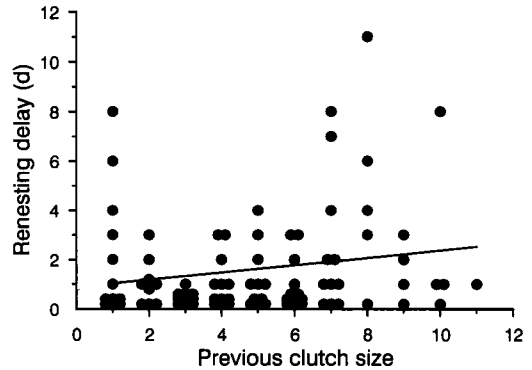


Fig. 1. Renesting delay of American Coots in relation to number of eggs in the previous clutch ($Y = 0.68 + 0.16X$, $r^2 = 0.04$, $P = 0.06$, $n = 92$).

quential eggs as any subset of total eggs that was produced in a single laying sequence and culminated in a completed clutch. Renesting delay refers to the number of days in which normal egg laying was delayed before initiating a replacement clutch; for instance, if a coot initiated a reneest on the day after clutch destruction, without missing a day of egg laying, the reneest interval was zero days. Coots lay eggs between 2400 and 0500 (Sooter 1941, Gullion 1954), well before I initiated field work. Hence, there was no danger of overestimating reneest intervals by one day due to birds having laid that day's egg after I had visited their nests.

Egg size was determined from linear measurements (± 0.05 mm) of length (L) and maximum breadth (B) using Hoyt's (1979) formula for estimated volume (cm^3):

$$V = 0.000507LB^2. \quad (1)$$

This measure of egg volume is highly correlated with fresh egg mass ($r^2 = 0.96$; Arnold 1991) and with total lipid, protein, and energy content ($r^2 = 0.51, 0.83$, and 0.78 , respectively; Arnold et al. 1991). Within-female and within-clutch repeatabilities for egg volume were determined using a nested ANOVA (Lessells and Boag 1987).

Statistical analyses were performed using the GLM and NESTED procedures of SAS (SAS Institute Inc. 1985), except F_{\max} -tests, which were computed by hand (Sokal and Rohlf 1973). Means ± 1 SD are presented. Regression lines were calculated using least squares.

RESULTS

Egg-removal experiments.—Coots that had six eggs experimentally removed from their nests during egg laying produced significantly more eggs than did unmanipulated controls (ANOVA on

pooled data, $P = 0.001$); however, they only replaced about one of the six missing eggs on average (Table 1). Removal effects were significant in 1985 and 1986 (Table 1), and were nearly significant in 1988 (feeding treatments pooled, $P = 0.09$), but egg removal did not affect clutch size among any of the 1987 feeding treatments (Table 1), or in the combined 1987 data ($P = 0.85$). Egg removal did not affect all coots uniformly; clutch sizes of most removal coots were similar to those of controls, but a significantly larger fraction of removal coots laid supernormal numbers of eggs (i.e. clutch sizes ≥ 13 , 25.7% of removal nests vs. 8.0% of control nests, Fisher exact test, $P = 0.00006$, Table 1). This heterogeneity of response to egg removals was reflected by among-treatment variance components. Variance in clutch size of removal birds increased relative to controls in seven out of eight sample groups (Table 1; sign test, $P = 0.03$); however, F_{\max} -tests were significant only for 1986 (un-supplemented), 1987 (corn-fed), and 1985–1988 (pooled data). There were no significant interaction effects between egg removal and supplemental feeding for either 1987 or 1988, or for both years combined, so the ability of coots to respond to egg removal did not appear to be a function of their ability to lay more eggs (according to the egg-formation hypothesis, supplementally fed birds should have been better able to lay more eggs). With data from all four years combined, there was a nearly significant removal-by-year interaction effect (Table 1, $P = 0.06$). Hence, the absence of a removal effect in 1987 reflected a statistically different population response to egg removal in comparison to the other three years.

When I included laying date as a covariate in the preceding analyses, quantitatively similar results were obtained in all but one case; removal effects for 1988 became statistically significant when date was used as a covariate (Table 1). There were significant removal-by-laying-date interactions in 1985, 1986, and 1988 (fed group only; Table 1). In 1985, the removal effect (i.e. mean removal clutch size minus mean control clutch size) became larger later in the nesting season, but during 1986 and 1988 the removal effect diminished later in the season.

In 1988, two coots responded to partial clutch removals by laying additional eggs in a second laying sequence. One coot laid 10 eggs, skipped four days, and then laid 3 more eggs. Another laid nine eggs, skipped from 2 to 12 days (pre-

cise interval unknown), and then laid four more eggs.

Egg-addition experiments.—In 1985 and 1986, clutch size was determined for six nests to which six eggs had been experimentally added during the laying period; one of these coots laid 9 eggs, two laid 10, and three laid 11 ($\bar{x} = 10.33 \pm 0.82$). Clutch size of addition nests did not differ from control nests (1985 and 1986 combined, 11.09 ± 1.61 , $n = 107$; F_{\max} -test, $F_{2,56} = 0.26$, $P > 0.05$; ANOVA, $F_{1,111} = 1.32$, $P = 0.25$).

Continuation nesting.—Most coots responded to complete clutch loss during laying by producing replacement clutches; 99 of 119 nests (83.2%) involving 73 different coots were known to be replaced (Appendix). Of the 20 clutches that were not replaced, 9 were destroyed after 10 June, by which time almost all nest initiations had ceased (including both initial nests and renests; Arnold 1990b). In addition, I had no opportunity to find replacement clutches for four nests in 1991 because subsequent nest searches were not conducted and there was no opportunity to observe potential broods.

Most continuation nests were initiated as part of the same laying sequence as the earlier clutch (65 of 92 intervals [70.7%]; Appendix, including three cases where females laid some parasitic eggs). The average re-nesting interval was 1.5 ± 2.2 days. Excluding nests for which destruction dates were imprecisely known, the average re-nesting interval was 0.8 ± 1.2 days ($n = 75$). Renest intervals increased slightly with number of eggs in the previous clutch (Fig. 1), but were unaffected by number of previous clutches ($b = 0.33$, $r^2 = 0.01$, $P = 0.31$) or total number of previous eggs ($b = 0.07$, $r^2 = 0.03$, $P = 0.10$).

Completed continuation nests averaged 9.1 ± 3.2 eggs in 1990 ($n = 23$) and 11.0 ± 2.3 eggs in 1991 ($n = 21$; Appendix), whereas completed first clutches averaged 9.7 ± 1.5 and 11.0 ± 2.1 eggs, respectively (Arnold 1990b, unpubl. data). These means did not differ (1990, $F_{1,93} = 1.60$, $P = 0.21$; 1991, $F_{1,136} = 0.00$, $P = 0.95$), even though continuation nests were initiated 12 and 5 days later, on average, than were 1990 and 1991 first clutches (1990, $F_{1,93} = 67.18$, $P \leq 0.0001$; 1991, $F_{1,135} = 22.78$, $P \leq 0.0001$). In 1990, initial clutch size declined by 1.0 egg over a 12-day period, whereas initial clutch size declined by 1.2 eggs over a 5-day period in 1991 (Fig. 2). In 1990, clutch size in continuation nests was nonsignificantly larger than clutch size in first nests after controlling for variation in laying date

(Fig. 2A; mean least squares for first nests, $\bar{x} = 9.48$; for continuation nests, $\bar{x} = 9.93$); in 1991, this effect became significant (Fig. 2B; mean least squares for first nests, $\bar{x} = 10.9$; for continuation nests, $\bar{x} = 11.9$). Further analysis revealed that the increase in clutch size of continuation nests in 1991 occurred only on fed wetlands (i.e. there was a significant food-by-nest-attempt interaction, $F_{1,131} = 4.96$, $P = 0.028$; mean least squares for unfed first nests, $\bar{x} = 10.6$; for unfed continuation nests, $\bar{x} = 10.8$; for fed first nests, $\bar{x} = 11.5$; for fed continuation nests, $\bar{x} = 13.8$). This interaction effect does not indicate that unfed coots had difficulty laying a normal-sized continuation clutch, but rather that fed coots were able to produce exceptionally large continuation clutches. Continuation nesters that initiated and completed their replacement clutch as part of the same laying sequence as their original clutch laid 13.3 ± 6.1 sequential eggs in 1990 (range 5–27) and 16.1 ± 4.3 sequential eggs in 1991 (range 9–24), an average of 3.6 and 5.1 eggs more than controls, respectively.

Coots that lost their clutches during egg laying produced more total eggs than did coots whose first clutches were undisturbed (1990 continuation nesters, 15.8 ± 8.2 eggs, range 2–35, $n = 32$ [data from Appendix]; 1990 undisturbed nesters, 9.7 ± 1.5 [Arnold 1990b]; 1991 continuation nesters, 12.8 ± 5.2 , range 3–24, $n = 41$ [Appendix]; 1991 undisturbed nesters, 11.0 ± 2.1 [Arnold unpubl. data]). If I excluded coots that never attempted to replace their initial clutch, coots that I collected during laying for other research, and coots whose territories were not searched for subsequent nests, the mean number of total eggs for continuation nesters was slightly larger (1990, 16.7 ± 7.6 ; 1991, 14.2 ± 5.0). In 1990, laying rates of continuation nesters increased with total number of eggs laid ($b = 0.010$, $F_{1,27} = 5.96$, $P = 0.02$), but declined with number of nesting attempts ($b = -0.105$, $F_{1,27} = 8.37$, $P = 0.007$), suggesting a significant temporal cost associated with production of nests rather than eggs. In 1991, laying rates of continuation nesters were significantly higher than in 1990 ($F_{1,61} = 7.16$, $P = 0.01$), but laying rates were not influenced by numbers of eggs or nests ($P = 0.43$ and 0.59 , respectively).

Egg-size variation.—Mean egg volume and clutch size were not correlated among removal nests ($r = 0.14$, $P = 0.24$, $n = 71$ nests). This correlation remained insignificant if it was based only on early-sequence (1–9) or late-sequence

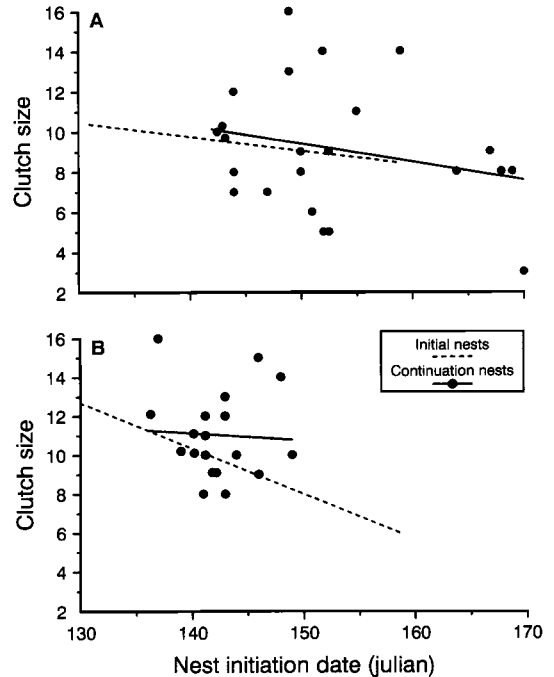


Fig. 2. Clutch sizes of initial and continuation nests in relation to nest initiation dates in (A) 1990 and (B) 1991. Regressions of clutch size on Julian nest initiation date: (A) 1990 initial clutches, $Y = 21.29 - 0.08X$, $r^2 = 0.07$, $P = 0.03$, $n = 68$; 1990 continuation clutches, $Y = 23.73 - 0.10X$, $r^2 = 0.08$, $P = 0.20$, $n = 23$. ANCOVA comparisons: clutch effect, $F_{1,90} = 0.54$, $P = 0.47$; date effect, $F_{1,90} = 6.99$, $P = 0.01$; interaction effect, $F_{1,89} = 0.04$, $P = 0.84$. (B) 1991 initial clutches, $Y = 42.96 - 0.23X$, $r^2 = 0.23$, $P = 0.0001$, $n = 117$; 1991 continuation clutches, $Y = 15.16 - 0.03X$, $r^2 = 0.002$, $P = 0.86$, $n = 19$. ANCOVA comparisons: clutch effect, $F_{1,133} = 4.24$, $P = 0.04$; date effect, $F_{1,133} = 30.64$, $P = 0.0001$; interaction effect, $F_{1,132} = 2.10$, $P = 0.15$.

(10⁺) eggs (early, $r = 0.14$, $P = 0.25$, $n = 70$ nests; late, $r = 0.10$, $P = 0.54$, $n = 38$ nests).

Egg size was highly repeatable between initial and continuation clutches; female effects accounted for 62.7% of the total variation in egg volume, whereas clutch effects accounted for only 13.1% of this variation. Egg size was not reduced among continuation clutches (mean egg size of second clutches averaged 0.47 ± 2.07 cm³ larger than in the initial clutch [representing a 1.7% increase]; paired t -test, $t = 1.54$, $P = 0.13$, $n = 46$ pairs). There was no trade off between total eggs laid by continuation nesters and mean egg size (Fig. 3).

Nest success.—Of 39 continuation nests that were completed and subsequently incubated,

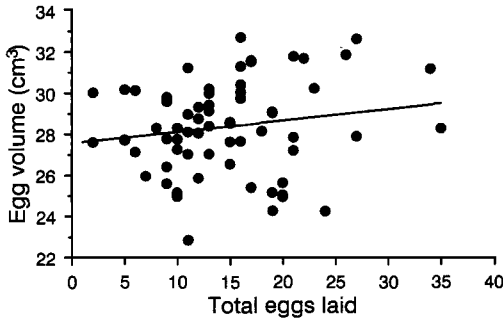


Fig. 3. Relationship between mean egg size and total egg production for American Coots losing one or more clutches during laying (data from Appendix). Trend line not significant ($r = 0.16$, $P = 0.20$, $n = 66$).

eggs in all but one successfully hatched (97.4%; data exclude one nest where I collected the female, three nests where final fate was not determined, and six "nests" that consisted only of brood observations), whereas apparent nest success of first nesting attempts in 1990 and 1991 (excluding nests that were abandoned or destroyed during laying, nests that I experimentally destroyed, and nests where I collected one or both of the adults) was 86.6% (123/142). This difference approaches statistical significance (Fisher's exact test, $P = 0.08$).

DISCUSSION

Egg-removal experiments.—During three of four years (1985, 1986, and 1988, but not 1987), coots laid larger clutches when six eggs were experimentally removed from their nests during egg laying. When variation due to laying date was statistically controlled, annual variation in response to experimental egg removal was nearly significant ($P = 0.06$). Thus, the lack of response in 1987 was not a statistical anomaly caused by small samples of nests; in fact, I obtained the most removal data in 1987. Such annual variation in response to egg removals might be predicted if coots had unusually low food supplies in 1987, or if they arrived on the breeding grounds with smaller lipid reserves than normal (Alisauskas and Ankney 1985) and, hence, were unable to produce as many eggs as in other years. Although mean clutch size was smaller in 1987 than in the preceding two years, it was somewhat larger than in 1988, when an effect of egg removal was detected. Coots did not arrive with larger lipid reserves in 1988 versus

1987 (Arnold 1990b; in fact, among laying females in 1987 fat and protein reserves were 3.3 and 7.3 g larger, respectively), and the failure of food supplements to enhance the removal effect in 1987 and 1988 suggests that local food supply was not an important determinant of a coot's "decision" to lay more eggs (see below). I cannot explain the lack of response to egg removals in 1987.

Although removal coots often laid more total eggs than did controls, they replaced, on average, only one of the six eggs that had been removed. There appeared to be pronounced individual variation in response to egg removals; some coots produced supernormal clutches (e.g. ≥ 13 eggs), whereas others laid as few as six total eggs. Individual variation in response to egg removals apparently was not a function of variation in access to food resources, because coots receiving supplemental food were no more likely to respond to partial clutch removals than were control coots. This failure to respond to food supplementation was not due to poor quality or inaccessibility of the food resources, because supplemental food did affect many other aspects of nesting biology (e.g. initial clutch size, fledging success, growth rate; Arnold 1990b). Reid (1987) obtained similar results when he supplied some Glaucous-winged Gulls (*Larus glaucescens*) with supplemental food and removed the first-laid egg on the day it was laid; some gulls laid a fourth egg, but their propensity to do so was unrelated to supplemental feeding.

Sooter (1941) removed all but one egg from 10 American Coot nests in Iowa. Two nests were immediately abandoned, but coots at the remaining eight nests went on to lay from 14 to 18 total eggs ($\bar{x} = 15.9$ vs. an average clutch size of 8.6 in comparable control nests). It is not clear from Sooter's (1941) account whether all eggs except the first were removed daily as laid, and whether all 14 to 18 eggs were laid as part of a single uninterrupted laying sequence. However, if both these conditions were met then it appears that his population was somehow better able to respond to egg removals, or that removals beginning with the second egg are more likely to be successful.

In European Kestrels (*Falco tinnunculus*), females will lay additional eggs only when removals are initiated before incubation constancy reaches about 50% (Beukeboom et al. 1988,

see also Meijer 1990). Meijer et al. (1990) hypothesized that the rising prolactin levels associated with onset of incubation are also responsible for suppressing the development of additional follicles and, hence, prolactin proximately determines clutch size. It is not known to what extent female coots incubate during egg laying (the issue is complicated by biparental incubation), or what happens to prolactin levels during the egg-laying period. However, incubation constancy increases steadily between day 3 and day 6 of egg laying, as determined from handling eggs and assessing their relative temperature (Bett 1983, Arnold unpubl. data), so perhaps initiating egg removals with the fourth-laid egg was not early enough to affect clutch size. Consistent with Meijer's view, removals were more effective in 1985–1986 than in 1987–1988, when natural clutch sizes were about two eggs larger (see Table 1). Thus, in 1985–1986, coots would have had two more days, on average, to respond to egg removals. The seasonal decline in responsiveness to egg removals, as evidenced by the negative interaction effect between egg removal and laying date in 1986 and 1988, also is consistent with this hypothesis. Clutch size declines seasonally and onset of incubation increases seasonally (Arnold 1990b, unpubl. data), so coots therefore have less time to respond to egg removals later in the season. Other birds also appear to exhibit a seasonal decline in responsiveness to egg removals (e.g. House Wrens [*Troglodytes aedon*], Kendeigh et al. 1956, Kennedy and Power 1990; captive American Kestrels [*Falco sparverius*], Porter 1975; Herring Gulls [*Larus argentatus*], Parsons 1976; European Kestrels, Beukeboom et al. 1988). Data on continuation nesting in coots would seem to invalidate the incubation/prolactin hypothesis of Meijer et al. (1990) because many birds re-nested immediately despite losing clutches of 6 to 11 eggs (Appendix); however, evidence suggests that prolactin levels may decline precipitously following partial or total clutch loss (Hall 1987a, b).

Two coots responded to egg removals by laying additional eggs, but only after several days of delay. These instances do not represent indeterminate laying, but are instead instances of double clutching in the same nest bowl. Such behavior has been observed previously among House Sparrows (*Passer domesticus*) in response to egg removals during laying (Anderson 1989),

and among American Coots in response to experimental reduction of clutch size during incubation (Fredrickson 1969), as well as at unmanipulated coot nests (Gullion 1954, Bett 1983, Hill 1986).

Results from the egg-removal experiments provided mixed support for the egg-formation hypothesis in American Coots. Although some coots responded to the removals by laying more eggs than they normally would have, most coots appeared unable or unwilling to replace the six eggs that had been removed. These results are similar to most other studies on determinacy of egg laying in precocial and semiprecocial birds, in which birds either failed to respond to egg removals or only responded in part (McAllister 1958, Barry 1962, Parsons 1976, Fugle and Rothstein 1977, Rohwer 1984, Winkler 1985, Reid 1987, Arnold 1990a; but for an alternative view see Kennedy 1991). When interpreting these studies, however, the distinction between being unable and unwilling to continue laying becomes crucial (Klomp 1970). If clutch size (total eggs to be laid) has been determined by the time that egg removals begin, then removals cannot test whether or not clutch size is limited by the ability of females to form eggs (Klomp 1970). Problems with timing of egg removals are not the only methodological concerns. Daily egg removals are designed to fool a laying female into "thinking" she has laid fewer eggs than she actually has, but some females might recognize these removals and interpret them as partial clutch predation. If such were the case, and if single-egg predators were likely to return to rob the remainder of the clutch, then the adaptive response to a perception of partial clutch reduction might be to abandon the current nest and begin a new nest elsewhere (e.g. Hall 1987a, Armstrong and Robertson 1988). In this scenario, egg-removal experiments cannot test the egg-formation hypothesis and will not indicate whether birds are determinate or indeterminate layers. Proximate physiological mechanisms of clutch-size determination (and when these occur) need to be better understood in order to properly interpret egg-removal experiments (Meijer 1990). Fortunately, studies of continuation nesting may help to resolve this issue in at least some species of birds.

Egg-addition experiments.—Coots did not respond to experimental egg additions by laying fewer eggs. Although my sample of addition

nests was small ($n = 6$), my chances of detecting reductions in clutch size of 1, 2, 3, 4, 5, or 6 eggs were 0.24, 0.70, 0.94, 0.996, 0.9999, and 1.00, respectively (Sokal and Rohlf 1973; one-tailed tests). Some authors have argued that it would be adaptive for birds to reduce their clutch size in response to intraspecific brood parasitism (Andersson 1984, Power et al. 1989; but see Rohwer and Freeman 1989). Although coots are regularly parasitized by conspecifics (Lyon 1991, Arnold unpubl. data), and there is evidence that survival is reduced among large broods (Lyon 1991), coots did not respond to experimentally enlarged clutches by laying fewer eggs. This is consistent with most other experiments that have added eggs to clutches during laying (reviewed by Kennedy 1991; but see Andersson and Eriksson 1982).

Continuation nesting.—In 1990, over 80% of all coot nests that were lost during laying were subsequently replaced with continuation nests. Only 7 of 92 renesting intervals (7.6%) were greater than five days, which represents the minimum amount of time necessary to develop new eggs from unenlarged ova (Alisauskas and Ankney 1985, Arnold 1990b). Hence, most coots initiated continuation nests by using follicles that were already developing. All long delays (i.e. > 5 days) followed nonmanipulative clutch losses, so that exact intervals between clutches were unknown. The majority of renest intervals were zero or one day. The length of renest intervals increased slightly with number of renesting attempts (one day for every three nests), number of eggs laid in the previous clutch (one day for every six eggs), and total number of previously laid eggs (one day for every 14 eggs). Although this may provide evidence that coots were becoming "exhausted" from continuation laying, the effect sizes, nevertheless, are quite small.

Some coots produced phenomenal numbers of consecutive or near-consecutive eggs: female 4029 laid 35 eggs in 37 days (four different nests plus two parasitic eggs); female 4018 laid 34 eggs in 39 days (five nests plus three parasitic eggs); and female 4009 laid 27 eggs in 28 days (three nests; Appendix). Other coots produced very large replacement clutches following a long laying series in one or more earlier nests: female 4088 laid a 17-egg clutch after laying 3 eggs in a previous nest; female 4029 laid a 14-egg clutch after laying 21 eggs in three previous clutches; and female 222 laid a 15-egg clutch after laying

8 eggs in two previous clutches (Appendix). Laying rates were not reduced among coots laying large numbers of eggs; in fact, these individuals had significantly faster rates of egg production in 1990. In contrast to these examples of excessive egg production, a few coots laid very small continuation clutches, and their combined total egg production was approximately one "normal" clutch of eggs (e.g. female 4094 laid four eggs in her first nest and only five eggs in a continuation nest; Appendix). Other coots had long renesting intervals (≥ 6 days; e.g. coots 4036, 4024, 4074, 4132, 56, and 140; Appendix) or experienced laying skips while producing the continuation clutch (coots 4005 and 4024). Collectively, these data on continuation nesting suggest that most coots had little difficulty in producing more than a normal complement of eggs, and that clutch size in most coots is unlikely to be limited by the ability to form eggs (cf. Alisauskas and Ankney 1985, Briggs 1989). However, a few coots apparently encountered difficulties while producing replacement clutches, and for these coots egg-formation costs may limit initial clutch size or renesting potential. Thus, I reject the egg-formation hypothesis as a single or primary explanation of clutch-size limitation in American Coots, although it may be important for some small portion of the population.

Results from my study suggest that continuation nesting is probably a better method than partial clutch removal for testing energetic limits on egg formation in coots. Rohwer (1986) arrived at a similar conclusion after comparing results from his own experiments on partial clutch removals in prairie dabbling ducks (Rohwer 1984) with anecdotal reports of continuation nesting in wild ducks. Continuation nesting may provide an alternative method of testing the egg-formation abilities of some other species of birds. For experiments on continuation nesting to be effective, birds must lay relatively large clutches, they must have access to alternative nest sites, nest construction must be rapid, and females must have ready access to mates displaying appropriate reproductive behavior. If birds lay small clutches with little time between successive eggs, and if follicles require several days to develop, then continuation nesting cannot occur rapidly unless birds develop supernumerary follicles, perhaps in anticipation of possible nest failure during the laying cycle. Although some birds do develop super-

numerary follicles (e.g. Hamann et al. 1986, Arnold unpubl. data; but see Astheimer 1986:fig. 5), it is not clear whether this represents an adaptation to possible nest destruction. The long egg-formation periods and small clutch sizes of most seabirds make them unlikely candidates for rapid continuation nesting (e.g. Astheimer 1986, Hatchwell and Pellatt 1990). Birds that nest in cavities or in dense colonies are unlikely to have access to alternative nest sites and, therefore, it is noteworthy that many of the best examples of indeterminate laying obtained via partial clutch removals have involved colonial- or cavity-nesting birds (e.g. Northern Flicker [*Colaptes auratus*], Phillips 1887; House Wren, Kendeigh et al. 1956, Kennedy and Power 1990; Wryneck [*Jynx torquilla*], references in Davis 1955; American and European kestrels, Porter 1975, Beukeboom et al. 1988; Herring Gull, Parsons 1976; Adelie Penguin [*Pygoscelis adeliae*], Astheimer and Grau 1985). Open-nesting passerines seem to require several days to construct a new nest (e.g. Nolan 1978) and, not surprisingly, most individuals losing nests during laying experience several days of delay before initiating a new laying cycle (Scott et al. 1987 and references therein). The small clutch size of most open-nesting passerines (i.e. 2-4), relative to egg-formation periods (ca. four days; Scott and Ankney 1983, Kremetz and Ankney 1986), may also preclude rapid continuation nesting. Continuation nesting is perhaps most likely to occur among solitary ground- or overwater-nesting species with relatively large clutches (e.g. some Podicipediformes, Ferguson and Sealy 1983, Arnold pers. observ.; Anseriformes, Rohwer 1986; Galliformes, Maxson 1977, K. Martin and S. J. Hannon pers. comm.; Rallidae, this study). Continuation nesting has been observed among Lapwings (*Vanellus vanellus*) that lost their original nests at the one-egg stage (Klomp 1970); these birds have proceeded immediately to lay a four-egg replacement clutch, thus producing five sequential eggs at a normal rate of laying. Egg-laying behavior analogous to continuation nesting has also been observed among inter- and intraspecific brood parasites (Scott and Ankney 1983, Gibbons 1986, Lyon 1991, J. M. Eadie, pers. comm., M. D. Sorenson, pers. comm.), and among birds with serial polyandry (Lank et al. 1985).

Egg-size variation and nest success.—Egg size was not markedly smaller among coots that laid large numbers of eggs in response to partial or

total clutch removals. Most previous tests of clutch size versus egg-size trade offs have relied on observational data comparing different species or comparing individuals within a population (e.g. Lack 1967, Rohwer 1988, Rohwer and Eisenhauer 1989). Such tests may not be valid, because different species (or individuals) may vary markedly in their access to resources. Those with abundant resources may invest more heavily in egg size and clutch size, whereas those with few resources may have to produce small eggs and small clutches. The result would be a positive correlation between the two traits, even though each was limited by food availability and, thus, by definition, part of a trade off. A better way to test for trade offs is to manipulate one variable and then assess variation in the second variable (Gustafsson and Sutherland 1988). In this study, I was able to manipulate the total number of eggs that individual coots laid and, yet, this had no discernable influence on egg size (or, vice versa, egg size had no influence on the number of eggs that coots were able to lay under experimental conditions). Other studies have also demonstrated no net decline in egg size in response to experimental manipulation of clutch size via egg removals (Kendeigh et al. 1956, Parsons 1976, Fugle and Rothstein 1977, Astheimer and Grau 1985, Astheimer 1986).

There was no evidence that birds laying additional eggs in continuation nests had lower nesting success; in fact, their nest success was probably higher than that of initial nesters (97 vs. 87%, respectively; $P = 0.08$). Because the two groups of nests exhibited minimal temporal overlap, the difference between the two groups could be attributable to a seasonal increase in nest success. It is clear that the data do not support the idea of an intraseasonal cost of reproduction associated with excessive egg production. I cannot assess possible costs that might have occurred during the brood-rearing or post-breeding seasons, but such delayed costs seem unlikely given that there were apparently no immediate costs of extended laying.

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LITERATURE CITED

- ALISAUSKAS, R. T. 1986. Variation in the composition of the eggs and chicks of American Coots. *Condor* 88:84-90.
- ALISAUSKAS, R. T., AND C. D. ANKNEY. 1985. Nutrient reserves and the energetics of reproduction in American Coots. *Auk* 102:133-144.
- ALISAUSKAS, R. T., C. D. ANKNEY, AND E. E. KLAAS. 1988. Winter diets and nutrition of midcontinental Lesser Snow Geese. *J. Wildl. Manage.* 52:403-414.
- ANDERSON, T. R. 1989. Determinate vs. indeterminate laying in the House Sparrow. *Auk* 106:730-732.
- ANDERSSON, M. 1984. Brood parasitism within species. Pages 195-228 in *Producers and scroungers: Strategies of exploitation and parasitism* (C. J. Barnard, Ed.). Croom Helm, London.
- ANDERSSON, M., AND M. O. G. ERIKSSON. 1982. Nest parasitism in Goldeneyes *Bucephala clangula*: Some evolutionary aspects. *Am. Nat.* 120:1-16.
- ANKNEY, C. D., AND A. D. AFTON. 1988. Bioenergetics of breeding Northern Shovelers: Diet, nutrient reserves, clutch size, and incubation. *Condor* 90:459-472.
- ANKNEY, C. D., AND C. D. MACINNES. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. *Auk* 95:459-471.
- ARMSTRONG, T., AND R. J. ROBERTSON. 1988. Parental investment based on clutch value: Nest desertion in response to partial clutch loss in dabbling ducks. *Anim. Behav.* 36:941-943.
- ARNOLD, T. W. 1990a. Determinacy of clutch size in Horned and Pied-billed grebes. *Wilson Bull.* 102:336-338.
- ARNOLD, T. W. 1990b. Food limitation and the adaptive significance of clutch size in American Coots (*Fulica americana*). Ph.D. dissertation, Univ. Western Ontario, London, Ontario.
- ARNOLD, T. W. 1991. Intraclutch variation in egg size of American Coots. *Condor* 93:19-27.
- ARNOLD, T. W., R. T. ALISAUSKAS, AND C. D. ANKNEY. 1991. Egg composition of American Coots in relation to habitat, year, laying date, clutch size, and supplemental feeding. *Auk* 108:532-547.
- ARNOLD, T. W., AND F. C. ROHWER. 1991. Do egg formation costs limit clutch size in waterfowl? A skeptical view. *Condor* 93:1032-1038.
- ASTHEIMER, L. B. 1986. Egg formation in Cassin's Auklet. *Auk* 103:682-693.
- ASTHEIMER, L. B., AND C. R. GRAU. 1985. The timing and energetic consequences of egg formation in the Adélie Penguin. *Condor* 87:256-268.
- BARRY, T. W. 1962. Effect of late seasons on Atlantic Brant reproduction. *J. Wildl. Manage.* 26:19-26.
- BETT, T. A. 1983. Influences of habitat composition on the breeding ecology of the American Coot (*Fulica americana*). M.S. thesis, Univ. Wisconsin, Oshkosh, Wisconsin.
- BEUKEBOOM, L., C. DIJKSTRA, S. DAAN, AND T. MEIJER. 1988. Seasonality of clutch size determination in the Kestrel *Falco tinnunculus*: An experimental approach. *Ornis Scand.* 19:41-48.
- BRIGGS, S. V. 1985. Patterns of egg-laying in prairie ducks. *Auk* 102:896-897.
- BRIGGS, S. V. 1989. Food addition, clutch size, and the timing of laying in American Coots. *Condor* 91:493-494.
- DAVIS, D. E. 1955. Determinate laying in Barn Swallows and Black-billed Magpies. *Condor* 57:81-87.
- DOTY, H. A., D. L. TRAUGER, AND J. R. SERIE. 1984. Renesting by Canvasbacks in southwestern Manitoba. *J. Wildl. Manage.* 48:581-584.
- DROBNEY, R. D., AND L. H. FREDRICKSON. 1985. Protein acquisition: A possible proximate factor limiting clutch size in Wood Ducks. *Wildfowl* 36:122-128.
- DUNCAN, D. C. 1986. Does food limit clutch size in prairie ducks? *Auk* 103:637-638.
- FERGUSON, R. S., AND S. G. SEALY. 1983. Breeding ecology of the Horned Grebe, *Podiceps auritus*, in southwestern Manitoba. *Can. Field-Nat.* 97:401-408.
- FREDRICKSON, L. H. 1969. An experimental study of clutch size of the American Coot. *Auk* 86:541-550.
- FUGLE, G. N., AND S. I. ROTHSTEIN. 1977. Clutch size determination, egg size, and eggshell thickness in the Pied-billed Grebe. *Auk* 94:371-373.
- GATES, J. M. 1962. Breeding biology of the Gadwall in northern Utah. *Wilson Bull.* 74:43-67.
- GIBBONS, J. W. 1986. Brood parasitism and cooperative nesting in the Moorhen, *Gallinula chloropus*. *Behav. Ecol. Sociobiol.* 19:221-232.
- GULLION, G. W. 1954. The reproductive cycle of American Coots in California. *Auk* 71:366-412.
- GUSTAFSSON, L., AND W. J. SUTHERLAND. 1988. The costs of reproduction in the Collared Flycatcher *Ficedula hypoleuca*. *Nature (Lond.)* 335:813-815.
- HALL, M. R. 1987a. Nesting success in Mallards after partial clutch loss by predators. *J. Wildl. Manage.* 51:530-533.
- HALL, M. R. 1987b. External stimuli affecting incubation behavior and prolactin secretion in the

- duck (*Anas platyrhynchos*). *Horm. Behav.* 21:269-287.
- HAMANN, J., B. ANDREWS, AND F. COOKE. 1986. The role of follicular atresia in inter- and intra-seasonal clutch size variation in Lesser Snow Geese (*Anser caerulescens caerulescens*). *J. Anim. Ecol.* 55:481-489.
- HATCHWELL, B. J., AND J. PELLATT. 1990. Intraspecific variation in egg composition and yolk formation in the Common Guillemot (*Uria aalge*). *J. Zool. (Lond.)* 220:279-286.
- HILL, W. L. 1986. Clutch overlap in American Coots. *Condor* 88:96-97.
- HILL, W. L. 1988. The effect of food abundance on the reproductive patterns of coots. *Condor* 90:324-331.
- HILL, W. L. 1989. Reply to Briggs: The roles of endogenous and exogenous nutrient supplies. *Condor* 91:494-495.
- HOYT, D. F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. *Auk* 96:73-77.
- JONES, J. C. 1940. Food habits of the American Coot with notes on distribution. U.S. Dep. Interior Wildl. Res. Bull. No. 2.
- KENDEIGH, S. C., T. C. KRAMER, AND F. HAMERSTROM. 1956. Variations in egg characteristics of the House Wren. *Auk* 73:42-65.
- KENNEDY, E. D. 1991. Determinate and indeterminate egg-laying patterns: A review. *Condor* 93:106-124.
- KENNEDY, E. D., AND H. W. POWER. 1990. Experiments on indeterminate laying in House Wrens and European Starlings. *Condor* 92:861-865.
- KLOMP, H. 1970. The determination of clutch size in birds, a review. *Ardea* 58:1-125.
- KREMENTZ, D. G., AND C. D. ANKNEY. 1986. Bioenergetics of egg production by female House Sparrows. *Auk* 103:299-305.
- LACK, D. 1947. The significance of clutch-size. Parts I and II. *Ibis* 89:302-352.
- LACK, D. 1967. The significance of clutch-size in waterfowl. *Wildfowl* 19:125-128.
- LANK, D. B., L. W. ORING, AND S. J. MAXSON. 1985. Mate and nutrient limitation of egg-laying in a polyandrous shorebird. *Ecology* 66:1513-1524.
- LESSELLS, C. M., AND P. T. BOAG. 1987. Unrepeatable repeatabilities: A common mistake. *Auk* 104:116-121.
- LIVEZEY, B. C. 1980. Effects of selected observer-related factors on fates of duck nests. *Wildl. Soc. Bull.* 8:123-128.
- LYON, B. E. 1991. Brood parasitism in American Coots: Avoiding the constraints of parental care. Pages 1023-1030 in *Acta XX Congressus Internationalis Ornithologici*. Christchurch, New Zealand, 1990. New Zealand Ornithol. Congr. Trust Board, Wellington.
- MAXSON, S. J. 1977. Activity patterns of female Ruffed Grouse during the breeding season. *Wilson Bull.* 89:439-455.
- MCCALLISTER, N. M. 1958. Courtship, hostile behavior, nest-establishment and egg laying in the Eared Grebe (*Podiceps caspicus*). *Auk* 75:290-311.
- MEIJER, T. 1990. Incubation development and clutch size in the Starling. *Ornis Scand.* 21:163-168.
- MEIJER, T., S. DAAN, AND M. HALL. 1990. Family planning in the Kestrel (*Falco tinnunculus*): The proximate control of covariation of laying date and clutch size. *Behaviour* 114:117-136.
- MØLLER, A. P., AND M. PETRIE. 1991. Evolution of intraspecific variability in birds' eggs: Is intraspecific nest parasitism the selective agent? Pages 1041-1048 in *Acta XX Congressus Internationalis Ornithologici*. Christchurch, New Zealand, 1990. New Zealand Ornithol. Congr. Trust Board, Wellington.
- NOLAN, V., JR. 1978. Ecology and behavior of the Prairie Warbler *Dendroica discolor*. *Ornithol. Monogr.* 26.
- PARSONS, J. 1976. Factors determining the number and size of eggs laid by Herring Gulls. *Condor* 78:481-497.
- PHILLIPS, C. L. 1887. Egg-laying extraordinary in *Colaptes auratus*. *Auk* 4:346.
- PORTER, R. D. 1975. Experimental alterations of clutch-size of captive American Kestrels *Falco sparverius*. *Ibis* 117:510-515.
- POWER, H. W., E. D. KENNEDY, L. C. ROMAGNANO, M. P. LOMBARDO, A. S. HOFFENBERG, P. C. STOUFFER, AND T. R. MCGUIRE. 1989. The parasitism insurance hypothesis: Why Starlings leave space for parasitic eggs. *Condor* 91:753-765.
- REID, W. V. 1987. Constraints on clutch size in the Glaucous-winged Gull. *Stud. Avian Biol.* 10:8-25.
- ROHWER, F. C. 1984. Patterns of egg laying in prairie ducks. *Auk* 101:603-605.
- ROHWER, F. C. 1986. Response to D. C. Duncan. *Auk* 103:638-639.
- ROHWER, F. C. 1988. Inter- and intraspecific relationships between egg size and clutch size in waterfowl. *Auk* 105:161-176.
- ROHWER, F. C., AND D. I. EISENHAEUER. 1989. Egg mass and clutch size relationships in geese, eiders, and swans. *Ornis Scand.* 20:43-48.
- ROHWER, F. C., AND S. FREEMAN. 1989. The distribution of conspecific nest parasitism in birds. *Can. J. Zool.* 67:239-253.
- RYDER, J. P. 1970. A possible factor in the evolution of clutch size in Ross' Goose. *Wilson Bull.* 82:5-13.
- SAS INSTITUTE. 1985. SAS user's guide: Statistics, version 5 ed. SAS Institute Inc., Cary, North Carolina.
- SCOTT, D. M., AND C. D. ANKNEY. 1983. The laying

cycle of Brown-headed Cowbirds: Passerine chickens? Auk 100:583-592.

SCOTT, D. M., R. E. LEMON, AND J. A. DARLEY. 1987. Relaying interval after nest failure in Gray Catbirds and Northern Cardinals. Wilson Bull. 99: 708-712.

SOKAL, R. R., AND F. J. ROHLF. 1973. Introduction to biostatistics, 2nd ed. W. H. Freeman, San Francisco.

SOOTER, C. A. 1941. Ecology and management of the

American Coot, *Fulica americana americana* Gmelin. Ph.D. dissertation, Iowa State Univ., Ames.

WINKLER, D. W. 1985. Factors determining a clutch size reduction in California Gulls (*Larus californicus*): A multi-hypothesis approach. Evolution 39:667-677.

WINKLER, D. W., AND J. R. WALTERS. 1983. The determination of clutch size in precocial birds. Curr. Ornithol. 1:33-68.

APPENDIX. Laying histories of American Coots experiencing total clutch losses during egg laying.*

Female	No. eggs laid in clutch					Interval (days) between clutches					Totals				Mean egg size (cm ³)	Nest success
	1	2	3	4	5	1-2	2-3	3-4	4-5	5-6	Eggs	Days	Lay rate	Nests		
1990																
4029	5	7	7	<u>14</u> ^b	—	<u>2</u> ^{cd}	2	0	—	—	35 ^d	37	0.946	4	28.26	Hatch
4018	6	6	7	4	8	<u>3</u> ^e	0	4	1	*	34 ^e	39	0.872	5	31.18	—
4009	3	10	<u>14</u>	—	—	0	1	—	—	—	27	28	0.964	3	27.88	Hatch
4036	10 ^f	8	4	5	—	8 ^g	3	3	*	—	27+	41	0.659	4	32.61	—
4026	3	7	1 ^h	6	<u>9</u>	0	7 ^h	1	2	—	26+	36	0.722	5	31.84	Hatch
4022	1	9	<u>13</u>	—	—	0	<u>1</u>	—	—	—	23	24	0.958	3	30.21	Hatch
4015	7	7	7	—	—	<u>1</u>	0	*	—	—	21	22	0.955	3	27.82	—
4005	11	9	—	—	—	<u>1</u> ⁱ	—	—	—	—	20	23 ⁱ	0.870	2	25.60	Hatch
4088	3	<u>16</u>	—	—	—	0	—	—	—	—	19	19	1.000	2	25.12	Hatch
4024	8 ^f	<u>11</u>	—	—	—	6 ⁱ	—	—	—	—	19+	27+	0.704	2	29.06	Hatch
4074	3	8 ^f	<u>8</u>	—	—	0	11 ⁱ	—	—	—	19+	30	0.633	3	24.24	Hatch
4011	5 ^f	<u>12</u>	—	—	—	1 ⁱ	—	—	—	—	17+	18	0.944	2	31.58	Hatch
4044	4	5	8	—	—	2	1	*	—	—	17	20	0.850	3	31.59	—
4006	6	<u>10</u>	—	—	—	0	—	—	—	—	16	16	1.000	2	30.41	Hatch
4025	6	<u>10</u>	—	—	—	0	—	—	—	—	16	16	1.000	2	29.74	Hatch
4012	6	<u>10</u>	—	—	—	0	—	—	—	—	16	16	1.000	2	32.70	Fail
4037	8 ^g	<u>8</u>	—	—	—	4	—	—	—	—	16	22	0.727	2	27.65	Hatch
4060	7	<u>8</u>	—	—	—	0	—	—	—	—	15	15	1.000	2	28.51	Hatch
4033	5	<u>8</u>	—	—	—	<u>2</u>	—	—	—	—	13	15	0.867	2	28.38	Hatch
4133	5 ^f	<u>8</u>	—	—	—	3 ^f	—	—	—	—	13+	16	0.813	2	29.12	Hatch
4082	5	<u>6</u>	—	—	—	2 ^f	—	—	—	—	12 ^a	13	0.923	2	28.04	Hatch
4046	5	7	—	—	—	4	—	—	—	—	12	16	0.750	2	29.31	Hatch
4055	2	9	—	—	—	<u>1</u>	—	—	—	—	11	12	0.917	2	22.84	Hatch
4080	6	<u>5</u>	—	—	—	3	—	—	—	—	11	14	0.786	2	28.96	— ^l
4027	3 ^f	<u>7</u>	—	—	—	1 ^f	—	—	—	—	10+	11	0.909	2	27.74	Hatch
4132	4 ^f	1 ^f	5	—	—	3 ^f	8 ^f	*	—	—	10+	21	0.476	3	24.95	—
4094	4	<u>5</u>	—	—	—	1	—	—	—	—	9	10	0.900	2	27.75	Hatch
4007	1 ⁱ	3	3	—	—	4	0	*	—	—	7	11	0.636	3	25.93	—
4080	3 ⁱ	2	—	—	—	0	*	—	—	—	5	5	1.000	2	30.15	—
4049	2 ^h	<u>3</u>	—	—	—	1	—	—	—	—	5+	6+	0.833	2	27.68	Hatch
4034	2 ⁱ	—	—	—	—	*	—	—	—	—	2	2	—	1	27.57	—
4084	2 ⁱ	—	—	—	—	*	—	—	—	—	2	2	—	1	29.99	—
1991																
149	10	<u>14</u>	—	—	—	<u>1</u>	—	—	—	—	24	25	0.960	2	24.23	Hatch
222	7 ^f	<u>15</u>	—	—	—	1 ^f	—	—	—	—	22+	23	0.957	2	31.66	Hatch
87	10	4	7	@	—	0	0	X@	—	—	21+	21+	1.000	3	27.18	Hatch@
144	7	1	<u>13</u>	—	—	1	0	—	—	—	21	22	0.955	3	31.76	Hatch
134	4	<u>16</u>	—	—	—	0	—	—	—	—	20	20	1.000	2	24.92	Hatch

APPENDIX. Continued.

Female	No. eggs laid in clutch					Interval (days) between clutches					Totals				Mean egg size (cm ³)	Nest success
	1	2	3	4	5	1-2	2-3	3-4	4-5	5-6	Eggs	Days	Lay rate	Nests		
225	6	<u>14</u>	—	—	—	3	—	—	—	—	20	23	0.870	2	25.01	Hatch
23	2	7	<u>10</u>	—	—	3	2	—	—	—	19	24	0.792	3	29.01	Hatch
46	8	<u>10</u>	—	—	—	0	—	—	—	—	18	18	1.000	2	28.11	Hatch
147	1	5	<u>11</u>	—	—	0	0	—	—	—	17	17	1.000	3	31.53	Hatch
203	4	<u>13</u>	—	—	—	<u>0</u>	—	—	—	—	17	17	1.000	2	25.39	Hatch
196	4	3	<u>9</u>	—	—	<u>0</u>	0	—	—	—	16	16	1.000	3	30.05	Hatch
162	6	<u>10</u>	—	—	—	0	—	—	—	—	16	16	1.000	2	31.30	Hatch
48	3	<u>12</u>	—	—	—	0	—	—	—	—	15	15	1.000	2	28.58	Hatch
152	4	<u>11</u>	—	—	—	1	—	—	—	—	15	16	0.938	2	27.62	— ⁿ
183	2	9	4	@	—	0	3	X@	—	—	15+	18+	0.833	4	26.54	Hatch@
123	9	5	@	—	—	2	@	—	—	—	14+	16+	0.875	3	—	Hatch@
160	1 ^h	<u>12</u>	—	—	—	0	—	—	—	—	13+	13+	1.000	2	29.97	Hatch
138	9	4 ^m	—	—	—	0	—	—	—	—	13+	13+	1.000	2	30.20	— ^m
168	3	<u>10</u>	—	—	—	0	—	—	—	—	13	13	1.000	2	27.02	Hatch
175	1 ^f	<u>12</u>	—	—	—	3 ^f	—	—	—	—	13+	16	0.813	2	29.41	Hatch
139	3	4	1	4	@	0	0	0	X@	—	12+	12+	1.000	5	28.74	Hatch@
40	2	<u>10</u>	—	—	—	1	—	—	—	—	12	13	0.923	2	25.84	— ^m
170	5	6 ^m	—	—	—	0	— ^m	—	—	—	11+	11+	1.000	2	31.21	— ^m
31	5	5	1	—	—	0	0	X	—	—	11	11	1.000	3	28.09	—
306	2 ^f	9	—	—	—	1 ^f	—	—	—	—	11+	12	0.917	2	—	— ⁿ
61	6	5 ^m	—	—	—	1	—	—	—	—	11+	12+	0.917	2	27.01	— ^m
193	6	4	@	—	—	0	X@	—	—	—	10+	10+	1.000	3	27.24	Hatch@
30	6	4	—	—	—	0	*	—	—	—	10	10	1.000	2	25.13	—
176	1 ^h	<u>9</u>	—	—	—	2 ^f	—	—	—	—	10+	12+	0.833	2	—	— ⁿ
56	7	3	—	—	—	8	*	—	—	—	10	18	0.556	2	28.29	—
192	1	<u>8</u>	—	—	—	0	—	—	—	—	9	9	1.000	2	26.39	Hatch
155	4	5	—	—	—	0	*	—	—	—	9	9	1.000	2	29.79	—
117	2	2	5	—	—	1	0	X	—	—	9	10	0.900	3	25.56	—
140	1 ^h	<u>8</u>	—	—	—	6 ^f	—	—	—	—	9+	15+	0.600	2	29.57	Hatch
171	2	6	—	—	—	2	X	—	—	—	8	8	1.000	2	28.28	—
93	7	—	—	—	—	*	—	—	—	—	7	7	—	1	—	—
187	6	@	—	—	—	X@	—	—	—	—	6+	6+	—	2	27.11	Hatch@
199	6 ^f	—	—	—	—	*	—	—	—	—	6+	6+	—	1	30.11	—
200	2	3	—	—	—	0	*	—	—	—	5	5	1.000	2	27.71	—
204	4 ^f	—	—	—	—	*	—	—	—	—	4+	4+	—	1	—	—
142	3	—	—	—	—	*	—	—	—	—	3	3	—	1	—	—

^a Estimates followed by + are minimal. *, no replacement nest found despite active searching. X, no nest search conducted. @, unmarked brood later sighted on territory, presumably from replacement clutch.

^b Complete (incubated) clutches underlined; all other clutches removed, destroyed, or abandoned during laying.

^c Renest intervals based on experimental clutch removals are underlined; all others from naturally destroyed or abandoned nests.

^d Two eggs laid parasitically in another coot's nest.

^e Three eggs laid parasitically in another coot's nest.

^f Exact day of clutch destruction unknown; clutch may have been complete and/or larger than indicated; renest interval may have been shorter than indicated.

^g Male killed on nest (probably by a Great Horned Owl, *Bubo virginianus*); female remated for second clutch.

^h Nest destroyed when found; estimates of eggs laid are minimums and estimates of renesting delays are maximums.

ⁱ Two additional laying skips within laying sequence for clutch 2.

^j Clutch 1 was a renest produced after an earlier clutch had been destroyed during incubation.

^k One egg laid parasitically in another coot's nest.

^l Nest experimentally destroyed to induce renesting.

^m Female collected for energetics study.

ⁿ Nest fate not determined.